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SPECIAL ASPECTS OF ENVIRONMENT RESULTING
FROM VARIOUS KINDS OF NUCLEAR WARS

PART II Annex III

Application of Input-Output Analysis
to a Homeostatic Ecosystem

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APPLICATION OF INPUT-OUTPUT ANALYSIS
TO A HOMEOSTATIC ECOSYSTEM

Input-output analysis is a technique which has been rather highly developed in economics.¹ It has been quite successful in making certain sorts of economic predictions, though it is not and does not purport to be a complete treatment of that subject.

In ecology it seems reasonable to conjecture that input-output analysis might also be appropriate in treating certain types of questions. In particular, one would like to ask such things as, "What level of insect feeding on crops would be likely to result if the insectivorous birds were driven away, all other conditions remaining unchanged?", or a more general version, "What is the likely consequence of such-and-such a selective pesticide removing some species and not others?"

Such questions not only have many obvious peacetime agricultural applications, but also bear on the design of sophisticated life-support systems and even one of the most difficult of all the problems involved in a study of a hypothetical postattack environment, namely the effect of a selective toxic agent (e.g. radioactive fallout) on the "balance of nature."

The possibility of using this type of analysis in the ecosphere depends on the fact that biological production is in fact limited by the availability of certain essential elements in the system, i.e., energy, water, nitrogen, phosphorus, carbon, etc. Where other factors are dominant, input-output analysis would clearly be inapplicable. For example, the rate of growth of bacteria in a culture or the nature of the biological succession in an "old field" are determined by dif-

ferent considerations. These are nonequilibrium problems.

Generally speaking, input-output would seem to be most appropriate where a homeostatic "steady-state" has been reached, either naturally (e.g. climax, vegetation) or as a result of the institutionalized permanent interference of man. By steady-state in this context we mean that a pattern is repeated year after year, on the average. The annual cycle of growth can perhaps be taken into account adequately by assuming a simple sinusoidal oscillation of the relevant variables with a one-year period. Biennial, triennial or quaterennial cycles (e.g. crop rotation schemes) could perhaps be handled in a similar way, but a simpler and perhaps equally valid procedure would be to average over a relatively homogeneous area (perhaps a county) and assume the distribution--percentage of land devoted to different crops--is constant from year to year even though the actual crops on a particular land-parcel may change.

In comparison, most other variations with time can either be averaged out or neglected, at least for an agricultural community or a complex temperate-zone ecosystem such as a mixed forest. This would apply to the day-night variation--a kind of high frequency "hum"--and to random short-term deviations from the average due to weather fluctuations--analogous to "noise". Long-term climatic fluctuations and low-frequency cyclic variations (e.g. the sunspot cycle and others) are somewhat harder to take into account. We will assume for the present that these variations have small amplitudes and can be neglected, although in some well known instances this assumption would clearly be faulty. An alternative procedure will be discussed which requires no assumptions regarding the time-behavior of the model ecosystem and can be

applied, in principle, even to non-homeostatic situations, at the cost of considerable labor.

§2 Development of the Model

Bases of Transactions: We focus attention on one of the elements being exchanged between various components of a biological system. A number of such elements exist, which may be labeled

ξ, η, ζ, \dots

For purposes of convenient reference, suppose ξ represents nitrogen; η , phosphorus; ζ , sulfur, etc. Carbon, water, energy, calcium et al. are all possible choices. In any particular case, our choice or choices of which elements are critical must be guided by prior knowledge of the system.

Components: The elementary components of any ecosystem are populations of individual species. In practice, however, much broader and more inclusive groupings are necessary if the problem is to be tractable (even with the help of electronic computers).

The optimal division of the system into lumped classes is not altogether well defined. Two criteria are important, neither of which necessarily would lead to the most aesthetically "natural" list of categories--which would differ for different biologists, but would probably be based in some sense on current understanding of phylogeny. It is vital to realize that for an input-output study phylogeny is essentially irrelevant. The two criteria are:

(1) If the model is to answer questions about some particular class, that class cannot be lumped into a larger group.

(2) The categories must be chosen in such a way that it makes

sense to describe an interaction between them in terms of exchange of one of the critical substances, e.g. ξ .

Point (1) is best illustrated by an example: if we are especially interested in the importance of bats in controlling night-flying insects, then both must appear explicitly, i.e., we cannot lump bats with mammals or vertebrates, and night-flying insects must explicitly be distinguished from other types.

Point (2) is less easy to explain precisely. The best illustration may be to give an example of an interaction which is not expressible in terms of exchanging any simple substance which has been mentioned so far: growth of the understory in a forest is determined primarily by the amount of light reaching it through the canopy. A division into "understory species" and "canopy species" would not satisfy the criterion unless ξ represented light--in which case most other interactions could not be expressed satisfactorily.

Assuming an appropriate division for the model ecosystem can be achieved, each class of components contains* a quantity of the basic exchangeable substances ξ, η, ζ, \dots . If there are N lumped classes in all, these quantities at any time are given by the variables

$$\begin{matrix} A_{1,\xi}^{(t)} & \dots & A_{N,\xi}^{(t)} \\ A_{1,\eta}^{(t)} & \dots & A_{N,\eta}^{(t)} \end{matrix}$$

For simplicity we shall discard the ξ, η, ζ subscripts in the following. Since ξ, η, ζ circulate constantly throughout the system, between any two arbitrarily chosen classes of components there is likely to be a net flow of the exchangeable substance in one direction of the other. Let us consider the flow of ξ between the j th and k th

*We use the word "contains" in lieu of a more accurate but cumbersome terminology. The operational definitions of the A_k 's are discussed in §4.

classes of components. This transfer is characterized by a coefficient or "matrix-element" a_{jk} which describes a channel having a uni-directional character, allowing ξ to move only from j to k . A channel in the reverse direction is described by a_{kj} and, in general, $a_{kj} \neq a_{jk}$. Here a_{jk} represents the fraction of all ξ -outgo from the j^{th} lumped-class going to the k^{th} lumped-class in a time increment δt . If we allow the possibility of internal transactions within a lumped-class, then the following relations must hold true if all interactions are taken into account:

$$\delta t \sum_{k=1}^N a_{jk} = 1 \text{ for all } j \quad 1a$$

where $a_{kk} \neq 0$ in general.

Open and Closed Systems; Reservoirs: Equation (1) characterizes a closed system in which the exchangeable substance ξ is conserved. Most ecosystems are (conceptually) open systems, however. That is, there is a constant shuttle back and forth between the (open) system and an external reservoir of ξ . The reservoir may be thought of, in general, as the soil, rocks, and the atmosphere, i.e., the inorganic world. It may be convenient to include the works of man, as well, unless production-consumption relationships are being investigated.

In an open system equation (1) will not hold; instead, there will be a system of inequalities

$$\delta t \sum_{k=1}^{N'=N-1} a_{jk} \leq 1 \text{ for all } j \quad 1b$$

The $N'=N-1$ notation indicates that one component (the reservoir) has been removed from consideration, whence transactions to and from the reservoir are omitted. Henceforth N will be used indiscriminately and distinctions (if any) between closed/open systems will be explicit.

The matrix a describes the transfer of ξ in the system in terms of the "sources" and "sinks" of ξ . One immediately obtains a set of equations:

$$\frac{\delta A^k}{\delta t} = \sum_{j=1}^N a_{jk}(A^j - A^k) \quad \text{for all } k \quad 2.$$

which expresses the fact that, in an increment of time δt any excess or deficit in the quantity of ξ contained in the k^{th} lumped-class of components, $\delta A_k(\xi)$ must have originated from the other $N-1$ components, or reappeared in them. Note that internal transactions a_{kk} do not contribute either way.

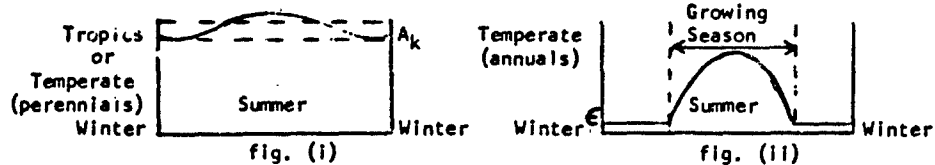
Continuous Cyclic Model: In the limit as $\delta t \rightarrow 0$, the equation becomes

$$\dot{A}_k = \sum_{j=1}^N a_{jk}(A_j - A_k) = \left(\sum_{j=1}^N a_{jk}A_j \right) - A_k \quad 3.$$

where \dot{A}_k is the time derivative of A_k and the a 's are now instantaneous rates. The most general time behavior of the system would be given by a Fourier integral:

$$A_k(\xi, t) = \int_{-\infty}^{\infty} A_k(\xi, \omega) e^{i\omega t} d\omega \quad 4a.$$

One thing we know about the system from the outset is that there exists a single overwhelmingly dominant frequency ω_0 with a period of one year, which expresses the most salient fact about the time behavior of the ecosystem: namely, the annual cycle. The best approximate time-function to pick depends on the climate and on the life cycles of the organisms making up each component. In the tropics the sinusoidal variation of a typical A_k is very slight, being superimposed on a non-zero average value, e.g. fig. (i):



The time-function corresponding to fig. (i) might be of the form

$$A_k(t) = \bar{A}_k [C_k + \cos \omega_0(t + \lambda_k)] \quad 4b.$$

In a temperate climate, the curves for annuals and perennials (both plant and animal) are quite different. The curve for most perennials resembles fig. (i), while that for annual species is more like fig. (ii); e.g. it is essentially zero during the winter months and rises sharply during the growing season, which spans the period between frosts. In the mid-continent U.S. at roughly 40° N. Latitude the growing season is quite close to 180 days or half of the year. For an ecosystem consisting largely of annual species at such a latitude, the time-dependence should be given by a function such as

$$A_k(t) = \bar{A}_k [C_k + \cos \omega_0(t + \lambda_k) \Theta_k(t)] + \epsilon \quad 4c.$$

where C_k is a constant depending on climate, ($C \approx 0$ at 40° N. Latitude in the midwestern U.S.), ϵ is a very small positive constant, and $\Theta_k(t)$ is zero when $C_k + \cos \omega_0(t + \lambda_k) < 0$, and unity otherwise.

For either (4b) or (4c) it is trivial to show that the integral of \dot{A} over a full cycle vanishes, viz.

$$\int_0^T \dot{A}_k(t) dt = A_k(T) - A_k(0) = 0 \quad 5.$$

where $T = 2\pi/\omega_0$. In an agricultural community in the temperate zone (e.g. Illinois) the choice (4c) with $C_k = 0$, seems most applicable. We shall assume this in the following for simplicity.

Similarly, we take

$$\alpha_{jk}(\xi, t) = \bar{\alpha}_{jk}(\xi) [\epsilon + \cos \omega_0(t + \gamma_{jk}) \Theta_{jk}] \quad 6.$$

where λ_k and γ_{jk} are unknown phase constants.

Note that $\Theta_k \Theta_{jk} = \Theta_s$ where Θ_s is unity over the range where both Θ_k and Θ_{jk} are unity, and zero elsewhere. Integrating over the cycle,

$$\int_0^T \Theta_s(t') dt' = \frac{\pi}{\omega_0} \left[1 - \frac{2\omega_0}{\pi} |\gamma_{jk} - \lambda_k| \right] \Theta_{k,k} = \frac{\pi}{\omega_0} \Lambda_{jk} \quad 7.$$

where $\Theta_{k,k}$ is equal to unity when the term in brackets is positive, and zero when it becomes negative. We therefore have, for the case $C_k = C_{jk} = 0$, and ϵ sufficiently small so that ϵ^2 can be neglected:

$$0 = \frac{1}{4} \sum_j \bar{A}_j \bar{\alpha}_{jk} \Lambda_{jk} \cos \omega_0 (\lambda_k - \gamma_{jk}) - \bar{A}_k \quad 8.$$

Note that Λ_{jk} always has the same indices as the argument of the accompanying cosine term, so the subscripts will be dropped henceforth. This is a set of linear homogeneous equations, if we treat $A_1 \dots A_n$ as unknowns. Nontrivial independent solutions exist only if the determinant of the matrix vanishes.

$$\text{Det } \bar{\bar{a}} = 0 \quad \text{where } \bar{\bar{a}}_{jk} = \bar{a}_{jk} \left[\frac{\Lambda}{4} \cos \omega_0 (\gamma_{jk} - \lambda_k) \right] - \delta_{jk} \quad 9.$$

If one of the A 's is fixed arbitrarily the remaining ones can be determined by straightforward methods. Altogether there are $N-1$ independent relations between the A 's and α 's and one involving only the α 's (equ. 9).

It should be noted that the continuous sinusoidal model, as we have derived it, cannot be applied without modification to a closed

system, though it is consistent with the assumption of an open system. This difficulty arises because equation (1) and equation (4)--derived from the requirement of ξ -conservation in a closed system--cannot be satisfied if all a 's and A 's have the simple sinusoidal behavior assumed in (4) and (6). A more complex time behavior would have to be assumed for at least one of the A 's and one of the a_{jk} 's (for each j).

Discrete Model: A different model is derivable from the basic equation (2) if the behavior of the ecosystem in time is considered to be a sequence of step-functions instead of a smooth variation.

Equation (2) can be rewritten

$$\frac{\delta A_k}{\delta t} = \frac{A_k(t + \delta t) - A_k(t)}{\delta t} = \sum_{j=1}^N a_{jk} (A_j(t) - A_k(t))$$

Whence (keeping δt finite),

$$A_k(t + \delta t) = \delta t \sum_{j=1}^N a_{jk} A_j(t)$$

or

$$A_k' = \delta t \sum_{j=1}^N a_{jk} A_j = \sum_{j=1}^N \beta_{jk} A_j \quad 10.$$

where the β_{jk} represent fractional transfer coefficients, rather than rates. Note that (10) can be iterated--thus the behavior of the system after any number of time increments is given by

$$\underline{A}^{(n)} = \underline{\beta}^{(n-1)} \dots \underline{\beta}^{(0)} \underline{A}^{(0)} \quad 11.$$

where the $\underline{A}^{(j)}$ are vectors and the $\underline{\beta}^{(j)}$ are matrices of rank N and

$$A_k^{(n)} = A_k(t + n\delta t)$$

Equations (11) supply nN equations for the $(n+1)N$ different $A_j^{(m)}(s)$, which is sufficient to determine all $A_j^{(m)}(s)$ for $m \neq 0$, assuming the set $A_j^{(0)}$ are given. Note that if the ecosystem undergoes a cyclic (annual or other) variation, the A_k must eventually return to the ori-

given set of values, after a time T made up of n increments:

$$A_k^{(n)} = A_k(t + T) = A_k^{(0)}(t) \quad 12.$$

whence

$$\prod_{j=0}^n \beta_{(j)} = 1 \quad 13.$$

(cycle)

or, in words, the products of n successive β -matrices over a single period in a cyclic variation must be equivalent to the unit matrix.

$$1 = \begin{pmatrix} 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \dots & \dots & 1 \end{pmatrix}$$

Equation (13) is the analog, in the discrete model, of the equation (7). It is equivalent to

$$\sum_{i(1)=1}^N \sum_{i(1)=1}^N \dots \sum_{i(n-1)=1}^N \beta_{j i(1)}^{(n-1)} \beta_{i(1) i(2)}^{(n-2)} \dots \beta_{i(n-1) k}^{(0)} = \delta_{j k} \quad 14.$$

Equation (14) supplies N^2 independent conditions between the nN^2 distinct matrix elements $\beta_{jk}^{(m)}$, while (11) supplies, in this instance, nN equations relating only nN different $A_j^{(m)}$ values, since $A_j^{(n)} = A_j^{(0)}$ for all j by the cyclic assumption. Thus a certain degree of simplification is introduced by the cyclic condition, but no assumption of a particular (e.g. sinusoidal) time behavior is made in this model. Moreover, if the cyclic condition is discarded, the discrete model can be applied to irreversible or non-cyclic types of time behavior.*

§3 Interpretation and Use of the Models

We have a number of entities (namely α 's, A 's and phase constants), most of which can, in principle, be measured directly

*Always provided the ecosystem's behavior is dominated by the interchange of some substance ξ .

or deduced from other data. Moreover there are a number of additional equations available relating the A's and d 's which can be used to reduce the number of independent pieces of data required.

One objective of our analysis is to examine how a perturbation affects the ecosystem. Many types of perturbation could be considered, but the simplest one which is not wildly unrealistic* is to assume that selective damage occurs which effectively eliminates one or more of the lumped groups of components without directly injuring the remainder. Our assumption about the simple time-dependence of the system would be invalid until the system had "settled down" in a new homeostatic equilibrium. We can ask, however, what the characteristics of the new system might be, i.e., the values of the A's and d 's after the perturbation.

Example: Consider, first, the continuous cyclic model and as an illustration take an ecosystem consisting of the following lumped-classes:

- Class 1. Vegetation (e.g. crops, weeds)
 - Decay organisms
- 2. Plant-feeding arthropods, nematodes, etc.
- 3. Predaceous and parasitic arthropods, nematodes, etc.
- 4. Vertebrates (birds, mammals, etc.)

The sample system is considered open, e.g. the total N-content is not fixed, but shuttles back and forth between the system and a nitrogen

*This type of perturbation is not inconsistent with what might happen if moderately heavy radioactive fallout were to cover the area as a result of a nuclear attack. It might be simulated in several ways: either by very active hunting or trapping of birds and mammals with perhaps the help of barriers and nets, or possibly by the use of certain poisons. It is known that birds and mammals are, on the average, considerably more radiosensitive than most insects, micro-organisms or plants of the grass family.²

"reservoir" which consists of the various inorganic sources (the soil, the atmosphere, the lithosphere, artificial fertilizers, etc.) and sinks (including ultimate consumers, e.g. man or livestock).

Let us now examine the matrix elements and see how many can be determined quickly. The various elements are as follows:

<u>Matrix Element</u>	<u>Interaction</u>
$a_{11}(1 \rightarrow 1)$	Reproduction, growth, decay of vegetation
$a_{12}(1 \rightarrow 2)$	Arthropod feeding on vegetation
$a_{13}(1 \rightarrow 3)$	—
$a_{14}(1 \rightarrow 4)$	Vertebrate feeding on vegetation
$a_{21}(2 \rightarrow 1)$	Decay of dead plant-feeders and metabolic wastes
$a_{22}(2 \rightarrow 2)$	Reproduction & growth of plant feeders
$a_{23}(2 \rightarrow 3)$	Predaceous or parasitic feeding on arthropods, etc.
$a_{24}(2 \rightarrow 4)$	Vertebrate feeding on arthropods, etc.
$a_{31}(3 \rightarrow 1)$	Decay of dead predators/parasites and metabolic wastes
$a_{32}(3 \rightarrow 2)$	—
$a_{33}(3 \rightarrow 3)$	{ Predation/parasitism on other predators/parasites Reproduction & growth of predators/parasites
$a_{34}(3 \rightarrow 4)$	Vertebrate feeding on predators/parasites
$a_{41}(4 \rightarrow 1)$	Decay of dead vertebrates and metabolic wastes
$a_{42}(4 \rightarrow 2)$	—
$a_{43}(4 \rightarrow 3)$	—
$a_{44}(4 \rightarrow 4)$	{ Vertebrate feeding on other vertebrates Reproduction & growth of vertebrates

It is immediately obvious that $a_{13} = a_{32} = a_{42} = a_{43} = 0$, since the corresponding interactions do not exist in the particular ecosystem being considered. Furthermore, it is quite reasonable to assume that $a_{21} \approx a_{31} \approx 0$, since few arthropods die a natural death; most are

consumed alive sooner or later by other arthropods or vertebrates. To a lesser extent this is also true of vertebrates, but among the dominant groups (birds and rodents) death by starvation is sufficiently frequent to warrant attention. We thus have

$$\begin{pmatrix} d_{11} & d_{12} & 0 & d_{14} \\ 0 & d_{22} & d_{23} & d_{24} \\ 0 & 0 & d_{33} & d_{34} \\ d_{41} & 0 & 0 & d_{44} \end{pmatrix} \quad \text{initial state}$$

As a consequence of the perturbation discussed earlier (mammals and birds destroyed), the last row and column would be missing in the perturbed matrix.

$$\begin{pmatrix} \tilde{d}_{11} & \tilde{d}_{12} & 0 \\ 0 & \tilde{d}_{22} & \tilde{d}_{23} \\ \tilde{d}_{31} & 0 & \tilde{d}_{33} \end{pmatrix} \quad \text{final state}$$

We allow for the possibility of a non-zero value for \tilde{d}_{31} . Since both matrices are time-dependent and the system is open, we have ten independent d 's and ten phase-constants to determine in order to specify the initial-state matrix completely. Six \tilde{d} 's and six phase-constants are sufficient to specify the final-state matrix.

Possible "Conservation Laws"

1. All phase constants remain unchanged, e.g.

$$\gamma_{ij} = \tilde{\gamma}_{ij} \quad \lambda_k = \tilde{\lambda}_k \quad 15.$$

assuming meteorological conditions remain the same.

2. One would tend to expect non-zero diagonal elements to remain unchanged, since the rate at which organisms in a given class reproduce, grow and/or feed on each other is unlikely to depend strongly on what happens elsewhere in the ecosystem. Thus (in the example),

$$a_{11} \approx \tilde{a}_{11}, a_{22} \approx \tilde{a}_{22}, a_{33} \approx \tilde{a}_{33} \quad 16.$$

3. Conservation of total ξ in a closed system. In this case equations (1) would be applicable and

$$\sum_{j=1}^N A_j = \sum_{j=1}^{N-1} \tilde{A}_j \quad 17.$$

In an open system, such as our particular example, modified approximate versions of (2) and (17) may still be available. Examination of each individual case is necessary. In the chosen example it seems reasonable to set

$$\max \sum_{j=1}^4 A_j = \max \sum_{j=1}^3 \tilde{A}_j \quad 18.$$

which expresses the likelihood that the maximum amount of protoplasm produced in the initial and final systems would be very nearly the same.

4. Functional relationships for ξ -transfers can be used if they are sufficiently simple and well established. In the chosen example, it seems reasonable to assume that the rate of arthropod feeding on plants is essentially proportional only to arthropod population, with the same proportionality before and after the perturbation. Thus,

$$a_{12}/A_2 \approx \tilde{a}_{12}/\tilde{A}_2 \quad 19.$$

which incidentally implies $\tilde{\gamma}_{12} = \lambda_2$ 20.

Admittedly the insect population depends indirectly on the amount of food available, but this may be thought of as a second-order rela-

tionship and is seldom limiting.* Initial conditions (number of overwintering larvae, etc.) and weather factors are, of course, averaged out in the model.

We also conjecture that the rate of arthropod predation and parasitism on other arthropods is approximately proportional to predator/parasite population, and that the ratios are conserved:

$$\alpha_{23}/A_3 \approx \tilde{\alpha}_{23}/\tilde{A}_3 \quad 21.$$

$$\text{This in turn implies } \gamma_{23} = \lambda_3 \quad 22.$$

A variety of equations describing functional interrelationships may be suggested for more complex ecosystems, but it must be recognized that the basis for many of them is likely to be theoretical, if not hypothetical, to a degree. To the extent that the number of possible equations involving the $\tilde{\alpha}$'s exceeds the number needed to determine completely the perturbed matrix, the more uncertain relationships can be tested against one another. This is not our present purpose, however, since the chosen example is too limited in scope to make such a sophisticated procedure seem likely to yield worthwhile results. It must be remembered, on the other hand, that in a more complex model there will be correspondingly more unknowns and the question of usefully interpreting some degree of overdetermination is moot.

For our example we can use the three equations (16), plus (18), (19) and (21), to fix the six independent $\tilde{\alpha}$'s. Thus the perturbed matrix is

*Odum et al.³ point out that insects seldom approach maximal feeding, whereas rodents often do. Presumably this reflects stricter supervision of insect populations by predators, and great sensitivity to weather conditions.

$$\begin{pmatrix} a_{11} & \tilde{a}_{12} & 0 \\ 0 & a_{22} & \tilde{a}_{23} \\ \tilde{a}_{31} & 0 & a_{33} \end{pmatrix}$$

From the earlier discussion of equation (9) it will be recalled that there is a linear homogeneous set of equations involving the time-independent amplitudes \tilde{a} defined by

$$\tilde{a}_{jk} = \tilde{a}_{jk} \left[\frac{1}{2} \Lambda \cos \omega_0(\tau_{jk} - \lambda_j) \right] - \delta_{jk}$$

and the amplitudes \tilde{A}_j . The conditional for solubility is $\tilde{a} = 0$, which becomes

$$0 = \left[\tilde{a}_{11} \left(\frac{1}{2} \Lambda \cos \omega_0(\tau_{11} - \tau_{12}) \right) - 1 \right] \left[\tilde{a}_{22} \left(\frac{1}{2} \Lambda \cos \omega_0(\tau_{22} - \tau_{23}) \right) - 1 \right] \times \\ \left[\tilde{a}_{33} \left(\frac{1}{2} \Lambda \cos \omega_0(\tau_{33} - \lambda_3) \right) - 1 \right] + \frac{1}{4} a_{12} a_{23} a_{31} \Lambda \cos \omega_0(\tau_{31} - \lambda_3) \quad 23.$$

In analogy to equation (8) we have

$$0 = \left[\tilde{a}_{11} \frac{1}{2} \Lambda \cos \omega_0(\tau_{11} - \tau_{12}) - 1 \right] \tilde{A}_1 + \tilde{a}_{31} \frac{1}{2} \Lambda \cos \omega_0(\tau_{31} - \lambda_3) \tilde{A}_3 \quad 24.$$

$$0 = \frac{1}{2} \tilde{a}_{12} \tilde{A}_1 + \left[\tilde{a}_{22} \frac{1}{2} \Lambda \cos \omega_0(\tau_{22} - \tau_{23}) - 1 \right] \tilde{A}_2 \quad 25.$$

$$0 = \frac{1}{2} \tilde{a}_{23} \tilde{A}_2 + \left[\tilde{a}_{33} \frac{1}{2} \Lambda \cos \omega_0(\tau_{33} - \lambda_3) - 1 \right] \tilde{A}_3 \quad 26.$$

Substitute (19) in (25) and (21) in (26), yielding

$$\tilde{A}_1 = 4 \frac{\tilde{A}_2}{\tilde{a}_{12}} \left[1 - \tilde{a}_{22} \frac{1}{2} \Lambda \cos \omega_0(\tau_{22} - \tau_{23}) \right] \quad 27.$$

$$\tilde{A}_2 = 4 \frac{\tilde{A}_3}{\tilde{a}_{23}} \left[1 - \tilde{a}_{33} \frac{1}{2} \Lambda \cos \omega_0(\tau_{33} - \lambda_3) \right] \quad 28.$$

Whence, using (19) again, we obtain

$$\tilde{a}_{12} = 4 \frac{\tilde{a}_{12}}{\tilde{a}_{23}} \frac{\tilde{A}_3}{\tilde{A}_2} \left[1 - \tilde{a}_{33} \frac{1}{2} \Lambda \cos \omega_0(\tau_{33} - \lambda_3) \right] \quad 29.$$

Q

Equation (18) calls for maximizing the sum of several sinusoidal functions with different phases. This would involve a good deal of rather tedious labor, and for the sake of simplicity we replace (18) by a relation involving amplitudes only:

$$K = \bar{A}_1 + \bar{A}_2 + \bar{A}_3 + \bar{A}_4 = \tilde{\bar{A}}_1 + \tilde{\bar{A}}_2 + \tilde{\bar{A}}_3 \quad 30.$$

We have introduced the constant K for convenience. From (27), (28) and (30) we obtain

$$\tilde{\bar{A}}_3 = K - 4 \left\{ \frac{\bar{A}_2}{\bar{a}_{12}} \left[1 - \bar{a}_{22} \pm \Lambda \cos \omega_0 (\bar{\tau}_{22} - \bar{\tau}_{23}) \right] + \frac{\bar{A}_3}{\bar{a}_{23}} \left[1 - \bar{a}_{33} \pm \Lambda \cos \omega_0 (\bar{\tau}_{33} - \bar{\tau}_3) \right] \right\} \quad 31.$$

Now insert (28) and (31) in (25) to get $\tilde{\bar{a}}_{23}$:

$$\tilde{\bar{a}}_{23} = 4 \frac{\tilde{\bar{A}}_3}{\bar{\lambda}_2} \left[1 - \bar{a}_{33} \pm \Lambda \cos \omega_0 (\bar{\tau}_{33} - \bar{\tau}_3) \right] \quad 32.$$

Finally, using (23), (29) and (32), we can determine $\tilde{\bar{a}}_{31}$. We shall not bother to exhibit $\tilde{\bar{a}}_{23}$ and $\tilde{\bar{a}}_{31}$ explicitly. This completes the formal analysis of the model ecosystem

Perhaps the most interesting result is equation (29), which determines the rate of insect feeding on vegetation in the perturbed case. Qualitatively, the conclusions can be stated: arthropod feeding in the perturbed case will be maximal for systems where arthropod predation and parasitism in the unperturbed case were minimal, as indicated by small populations (\bar{A}_3) and small growth potential (\bar{a}_{33}). The greater the difference between the phases $\bar{\tau}_{33}$ and $\bar{\tau}_3$, the greater the effect of insect feeding in the perturbed case.

It would be interesting and instructive to carry through a graphical analysis of the equations. It would also be desirable to use the iterative step-function approach on the same model ecosystem--perhaps assuming four discrete increments of three months each.* However, the mathematical complexity of the job is rather higher than was the case with our chosen example, and it might pay to program the iteration for a computer and go to a much larger number of iterations. Here the objective would probably have to be to follow the actual time behavior of a system where a sufficient number of matrix elements was known explicitly as functions of time. Predictions could be made of the behavior of the remainder. Our more ambitious objective of predicting the response of an ecosystem to perturbation seems beyond the scope of the discrete model (simply because less is assumed and more has to be calculated).

§4 Sources of Data

To complete the illustration we shall outline a number of possible data sources or experiments. Care must be exercised to choose sufficiently many Independent sources, e.g. it would be inconsistent to measure two quantities related by a "conservation equation" separately, while using the equation.

It is important to keep in mind that A_k is not simply the § (e.g. nitrogen) content of the standing crop of the k^{th} class. No allowance need be made in the continuous model for that portion of the standing crop

*Actually there is no particular advantage in choosing equal time periods. The technique permits great flexibility in the choice of increments.

which is "consumed" by the ecosystem, but the portion excreted or used up in metabolic processes must be counted as though it were still physically present. On the other hand, in the discrete model the potential crop during a given increment of time must also be considered, and if the time increments are considerable, the necessary corrections to allow for turnover may be sizable.

In the case of grain crops the potential crop during a growing season is probably of the order of 20-25% larger than the actual crop,⁴ but there is no N-excretion.* In the case of short life-cycle organisms the difference may be much greater. Odum *et al.*⁵ estimate the biomass of the potential crop of grasshoppers in an old-field ecosystem to be of the order of 10 times the observed maximum standing crop at peak periods (an estimate which is, admittedly, uncertain at best). Unfortunately, census counts are only suitable for measuring the standing crop, whence, from the point of view of collecting useful data, the continuous model must be preferred. Even here the difficulties are severe. One vexatious problem is to deduce the total population from the size of a series of samples, since an absolute count is generally infeasible, if not impossible, for arthropods and other small organisms. Some recent work indicates that real progress is being made in overcoming these difficulties,⁶ but results are preliminary so far. Moreover metabolic losses of nitrogen in excreta are difficult to measure in many cases (e.g. arthropods) and this fact introduces further uncertainties.

To make the problem concrete, let us specify a particular ecosystem for which existing data are reasonably concrete, namely a homogeneous grain farming area such as Champaign county, Illinois. Much

*If we were tracing the H₂O economy, transpiration would be important.

basic information is available in publications of the College of Agriculture of the University of Illinois.⁷ For the particular county in question the average crop mix is 43.2% corn, 31.2% soybeans, and much smaller percentages in oats, wheat, forage and woodland. The "growing season"--measured arbitrarily from the mean date of the last spring freeze to the mean date of the first fall freeze--embraces the period April 25 to October 20 (~180 days).

The influence of bioclimatological factors on phenology has been investigated comprehensively by the American Institute of Crop Ecology.⁸ It has been found that growth and maturity can be indexed quite accurately in terms of the number of day-degrees* elapsed between different stages. Extrapolating some of these results to the soil and climate of Champaign county (using the local conditions to "normalize") should make it possible to estimate with reasonable accuracy, apart from the contribution arising from decay organisms. Unless it is desired to focus attention on the decay process explicitly, almost any reasonable assumption can be made regarding the latter, providing only that consistency is maintained. In fact, in an open model the decay process can be lumped with the external interactions (the reservoir) and ignored altogether, providing the interpretation of α_{11} is consistent.

Other data of a rather cruder sort are also available in the literature. For example, there exist estimates of the net primary production (in grams) of various crops under different conditions.⁹ For corn, in particular, Illinois approaches the ecological optimum with yields of 1011 grams per square meter per year, or 5.6 grams per square meter per day during the 180-day growing season.¹⁰ These figures must, of course, be translated into N-content but many analyses

*Measured above a 40° F. base.

of the chemical composition of various plant parts, for various crops, are available.¹¹ These integrals average out the time-dependence of the quantities in question but are useful as a means of double checking. By working backwards (if the sinusoidal time behavior is assumed) the amplitude A_1 can be deduced independently--at least for corn. Still other types of data are available, such as detailed measurements of N-uptake from soils by various crops. Here, of course, allowance must be made for contributions by N-fixing bacteria living in the soil.¹²

If a forest were being considered the estimates would be more difficult to make. A recent technique has been discussed wherein CO_2 production is measured and used as an index of metabolism.¹³ Estimates of the standing crop in terms of canopy foliage, understory foliage, woody parts, etc. have been made.

Standing crops of arthropods and other animals are much more difficult to estimate and subject to much greater fluctuations. For farmlands the best source of primary data on grazing insects is probably the Cooperative Economic Insect Report.¹⁴ Beneficial insects are also occasionally reported, but evidently less thoroughly.

Obtaining the N-content of body material plus wastes is also a problem, especially for arthropods, since protein percentage alone is not a reliable guide in this case.* Unfortunately the typical arthropod exoskeleton (integument, or chitin) has a molecular structure in which certain N-containing amino acids are linked tightly to long-chain molecules similar to cellulose. Both the N-content and, more important, the absolute quantity of integument vary widely from species

*As a rule of thumb, on a dry-weight basis protein averages 16% nitrogen.

to species, making extrapolations from the few well known cases¹⁵ difficult. In spite of the problems, however, it should be possible to estimate A_2 with reasonable confidence, though there are probably insufficient census data to obtain A_3 .

Losses of crops by insect feeding are also estimated from time to time by the USDA in terms of a percentage of the monetary value of the national harvest.¹⁶ To the extent that national averages are applicable to the chosen geographical area, and to the extent that damage to the seed or fruit portion of the crop reflects damage to other portions, some sort of estimate for α_{12} might be derived. Since the seed or fruit constitutes a small percent of the total plant protoplasm (averaging 7% for herbaceous annuals and grasses)--which, however, varies considerably from species to species--and since arthropods as a class do not feed on all plant parts equally (though their exact degree of preference for the more succulent parts would be difficult to estimate quantitatively), there are very many uncertainties in this type of calculation. Laboratory or greenhouse experiments may be possible which would aid in these determinations, especially as regards the composition of body wastes, although it can be extraordinarily difficult to simulate field conditions. Another possible avenue is the use of radio-isotopes as tracers. A number of projects using tracer techniques are under way at present, at Oak Ridge National Laboratory and at the University of Minnesota, among others. It seems possible that some of their data may be applicable to the present problem, even though the experiments were carried out with different objectives in view. Tracer techniques may offer the only practical possibility of determining A_3 .

and with a good deal of refinement it is conceivable that an approximation for α_{23} could be obtained.

The two dominant vertebrate populations are likely to be the birds and rodents. Bird populations are strongly influenced by the presence or absence of cover (woodlands or large trees) and in Champaign county, where only 1.3% of the land is wooded, suitable nesting sites are somewhat limited. An average of 3 birds per acre has been estimated for Illinois farmlands,¹⁷ including horned larks, starlings, crows, nuthatches, bluejays, cardinals and a number of other species. Census counts are made by numerous local birdwatching clubs and kept in the archives of the National Audubon Society. The Bureau of Biological Survey is another, perhaps more reliable, source, both for birds and other animals.¹⁸ Counts of rodents, shrews, voles, moles, bats, skunks, etc. are probably an order of magnitude less complete and may be altogether inadequate. However, direct experimental verification in geographically limited areas should not be unduly difficult, since the ground-living animals (unlike birds) may be considered essentially immobile. N-content of warm-blooded animals is not difficult to compute from the weight, but metabolic losses (excreta) are dominant. An average 4 oz. meadowlark is likely to consume about 24 times its own weight in food each year, and a $\frac{1}{2}$ oz. shrew may consume two or three times its own weight per day. Detailed correlations between body weight and metabolic rate for warm-blooded animals are available in the literature¹⁹, whence extrapolations from one species or one stage in the life cycle to another should be within the scope of possibility. The diets of at least some common species have been studied with consid-

erable care. Very detailed analyses of the seasonal variation of the stomach contents of the common crow and starling have been published,²⁰ and others doubtless exist. By thorough analysis of available data, and perhaps a minimal addition of new data, it should be possible to estimate A_4 , d_{41} , d_{14} , d_{24} , d_{34} and d_{44} .

In summary, it appears feasible to obtain more or less direct experimental evidence which would be capable of yielding numerical values for most of the A 's and d 's. However, in view of the uncertainties involved, one would feel relatively little confidence in determinations of d_{12} , d_{23} , d_{22} , d_{33} , A_2 and A_3 . Either functional relationships relating some of the elements, e.g.

$$A_1 + A_2 : A_3 + A_4 = K$$

30.

$$d_{12} = K'A_2$$

$$d_{23} = K''A_3$$

analogous to (19) and (20) must be used, or uncertain numerical estimates must be accepted. In practice, the best procedure would probably be to iterate the solutions by repeating the calculations using different sets of assumptions until the maximum degree of self-consistency is achieved. Ultimately, of course, better techniques of experimental verification must be found.

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